

RESEARCH

Long-Term Surveys Show Invasive Overbite Clams (*Potamocorbula amurensis*) are Spatially Limited in Suisun Marsh, California

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ABSTRACT

The overbite clam (*Potamocorbula amurensis*) is a major invasive species in the San Francisco Estuary, California, and has been implicated in the decline of pelagic productivity and native fish species. Little is known of its impact on Suisun Marsh, a large brackish tidal region of the estuary. We looked at the abundance and spatial distribution of clams in the marsh, including examining the influence of water quality, using long-term (1988–2015) otter trawl surveys. Temporal trends indicated that overbite clam abundance has been increasing, but adult clams were spatially restricted to a single large slough (Suisun). Clams were absent from most interior channels, limiting their overall effect on the marsh aquatic ecosystem. Abiotic variables, particularly salinity, proved important predictors of overbite clam abundance, although the variables examined alone could not explain overbite clam distributions. We propose that connectivity, detritus loads, and/or predation pressure may work in conjunction

with abiotic variables to cause poor survival rates for recruits in interior marsh sites, keeping the distribution limited. Overall results are encouraging for restoration projects in brackish tidal marshes that need to deal with overbite clams.

KEY WORDS

Bivalve, salinity, otter trawls, GAM models, wetlands, restoration

INTRODUCTION

Non-native bivalves have been introduced into many estuaries, with significant consequences to aquatic communities (Sousa et al. 2009). Many of these species are extremely prolific, are adaptable, and are highly efficient predators on plankton (Alpine and Cloern 1992; Dame 1996; Pace et al. 1998; Strayer et al. 1999). Non-native bivalves have also led to substantial declines in phytoplankton biomass, and have reduced zooplankton recruitment and abundance in estuaries (Kimmerer et al. 1994), ultimately altering food webs and reducing pelagic fish abundances (Kimmerer 2006; Miehl et al. 2009). As a result, prevention and control of bivalve invasions has become a priority in estuarine management.

One such system experiencing altered food-web dynamics and serious depletions in phytoplankton is the San Francisco Estuary (the estuary) (Nichols et al. 1990; Greene et al. 2011). This large estuary

suffers from immense anthropogenic effects and, as a global shipping and receiving port, an increasing susceptibility to invasive species (Grosholz 2002; Cloern and Jassby 2012). At least three alien bivalves have been introduced into the estuary, with the overbite clam (*Potamocorbula amurensis*) being the most abundant (Cohen and Carlton 1998). Overbite clams were first captured in the estuary in 1986, and later in the more inland Suisun Marsh in 1988 (Carlton et al. 1990). The clams quickly expanded throughout the estuary's brackish waters and became a dominant benthic species (Nichols et al. 1990; Alpine and Cloern 1992; Peterson and Vayssières 2010). With efficient filtering capabilities and high densities, overbite clams have been responsible for considerable declines in phytoplankton biomass in the estuary (Greene et al. 2011). Following their introduction, a steep decline was observed in some pelagic organisms, including fish. The decline became especially evident around 2002 and is commonly referred to as the Pelagic Organism Decline (POD) (Sommer et al. 2007).

One reason for the overbite clam's success in the estuary is that reproduction occurs year-round, although reproduction is temporally restricted in some regions of the estuary (Parchaso 1993; Parchaso and Thompson 2002). For example, in Grizzly Bay (Figure 1) reproduction occurs in late spring/early summer and again in fall (Parchaso and Thompson 2002). Overbite clams are broadcast spawners, reaching sexual maturity at approximately 5-mm shell width (2 months after recruitment). They generally live 2 to 2.5 years, reaching a maximum shell width of 26 mm (Hymanson 1991; Parchaso and Thompson 2002; Thompson et al. 2008). Larvae are found in the water column from Day 2 up to Day 19 post-hatch, and have increasing behavioral control of their position in the water column starting on Day 7 (Nicolini and Penry 2000).

Multiple biotic and abiotic factors affect overbite clam survival in the estuary (Hymanson 1991). Predation is one factor: diving ducks and fish cause observable declines in overbite clams in shallow waters during winter (Lovvorn et al. 2013). Salinity is generally thought to be the primary abiotic factor that controls the clam's large-scale distribution and abundance in the estuary. Based on field and laboratory observations, salinities of ≥ 5 ppt are

necessary for persistence of clams in the estuary (Werner et al. 2003). Successful spawning and fertilization takes place at 5 to 25 ppt (Hymanson 1991; Nicolini and Penry 2000). However, adults persist in a salinity range of 0.1 to 32 ppt (Carlton et al. 1990). Miller and Stillman (2013) examined metabolic rates in adult clams and did not detect changes in metabolism at near-freshwater conditions, which supports their having a high degree of tolerance for a wide range of salinities. Lack of metabolic response to temperature and food availability was also noted. Thus, the authors concluded salinity and temperature did not influence distribution and abundance of adult overbite clams.

Though the overbite clam has been well-studied in bays and mainstem river channels of the estuary, little is known of its long-term abundance, distribution, or potential ecological effects in Suisun Marsh, a large brackish tidal marsh with important juvenile fish habitat (Moyle et al. 2012, 2014). Using ancillary data from a large-scale 35-year fish study, we investigated overbite clams in Suisun Marsh to answer three basic questions:

1. What is the abundance trend of overbite clam in Suisun Marsh since 1988, the year they were first detected?
2. What is the spatial distribution of overbite clams in Suisun Marsh?
3. What environmental parameters predict overbite clam abundance?

METHODS

Study Area

Suisun Marsh is a large (~34,000 ha) brackish tidal marsh between the Sacramento–San Joaquin Delta and San Pablo Bay (Figure 1). Suisun Marsh is recognized as being an important low-salinity habitat for numerous fishes and invertebrates (Meng et al. 1994; Meng and Matern 2001; Matern et al. 2002; Feyrer et al. 2003). Although Suisun Marsh has been invaded by numerous alien species (Matern et al. 2002; Schroeter 2008), it still has areas of high phytoplankton biomass (Mueller–Solger et al. 2002) and a relatively stable brackish fish community of

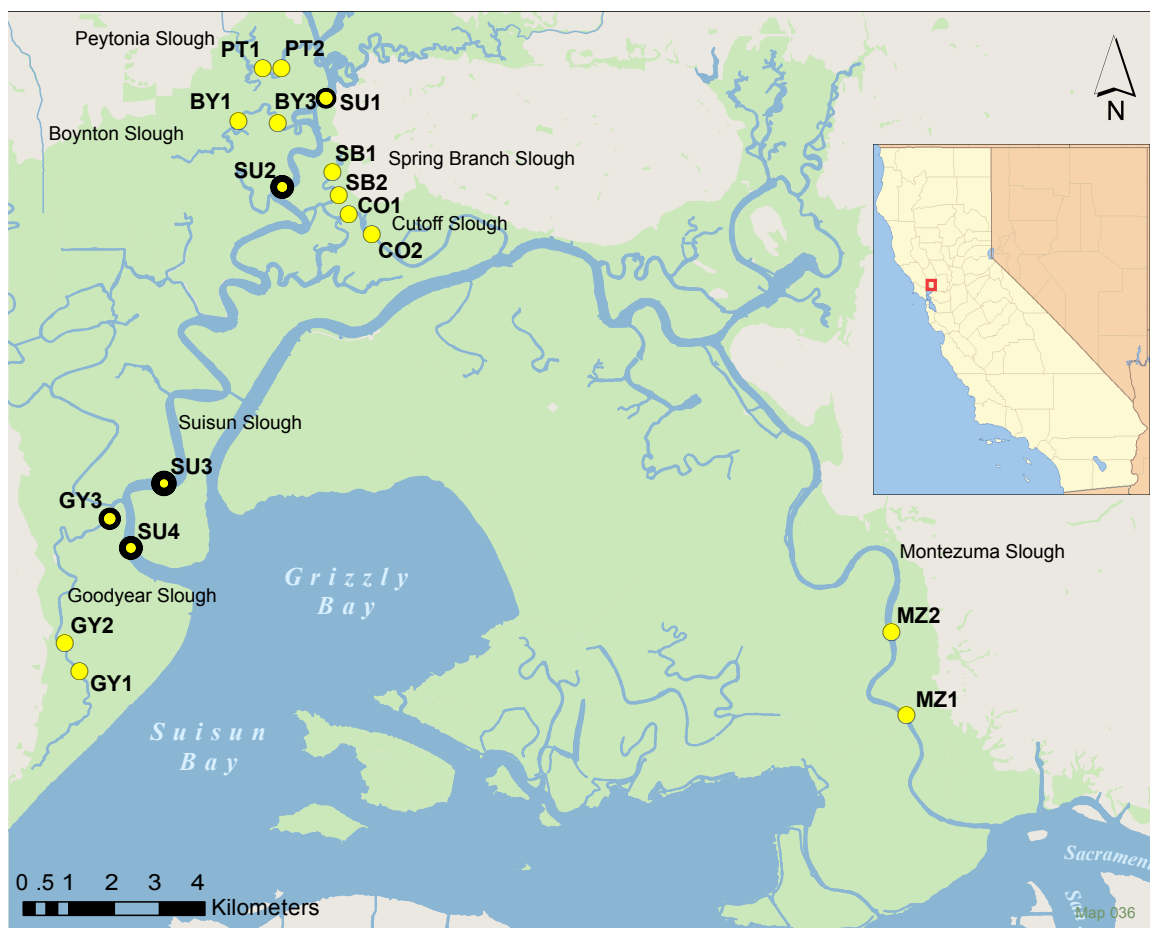


Figure 1 Locations of 17 otter trawl sampling sites in Suisun Marsh. Border thickness indicates general abundance of clams.

both alien and native fishes (Matern et al. 2002; Schroeter 2008; Moyle et al. 2014).

Sample Collection

Overbite clams were collected by otter trawl as part of a long-term fish monitoring project in Suisun Marsh (Matern et al. 2002). Since overbite clams were not detected in Suisun Marsh until 1988, data from 1980 to 1987 were excluded from our study. Trawling was conducted monthly at 17 stations situated throughout the marsh using a four-seam otter trawl (Figure 1; trawl height = 1.5 m, width = 4.3 m, length = 5.3 m; body net mesh 35-mm stretch, cod-end mesh 6-mm stretch). The trawl was towed during daylight hours at 4 km hr^{-1} for 5 or 10 minutes, depending on slough size (width and depth). Small sloughs were sampled for 5 minutes (Spring Branch, Peytonia, Goodyear, Cutoff, Boynton),

and large sloughs (Suisun and Montezuma) were sampled for 10 minutes. At the end of each trawl, organisms were identified, counted, and released at the site of capture. Trawl mesh retained overbite clams approximately 20 mm or larger throughout the body of the trawl, down to a minimum size of approximately 5 mm in the cod-end (i.e., adult-sized clams). Standardized sampling protocols and the large number of samples collected over 27 years (5,508 samples) provide a robust measure of the relative abundance of adults ($>5 \text{ mm}$). All catch results were converted to catch per minute (catch minute^{-1}) to standardize catch for both small and large sloughs. Water-quality data were recorded at the conclusion of each tow. Water transparency was measured with a Secchi disc (cm); temperature ($^{\circ}\text{C}$), specific conductance (microSiemens: μS), and salinity (ppt) were measured using Yellow Springs Instruments (YSI) hand-held meters (models 85 and 95). Dissolved

oxygen parameters (DO: mg L⁻¹ and % saturation), first sampled in 2000, were also measured with the YSI meters.

Analyses

To evaluate long-term patterns in abundance, we conducted a Mann–Kendall test (R software system, R Package Kendall; Kendall and Gibbons 1990; McCleod 2011). The Mann–Kendall trend test is a non-parametric rank-based test effective for identifying monotonic data trends when extreme values and skewness are present (Helsel and Hirsch 1992). We standardized catch data to catch minute⁻¹ and log⁺¹ transformed before analyses to better approximate the constant variance required for a Mann–Kendall test.

To assess the spatial distribution and to look for distributional shifts over the 27-year study, we plotted annual catch by site. Overlaying spatial data with abundance provided a visual assessment of their relationship.

To determine the functional relationship between catch patterns and water-quality metrics, we performed generalized additive modeling (GAM; R software system, R package MGCV). GAM models account for non-linear relationships common in ecological data by utilizing smoothing functions to determine the relationship between variables (Zuur 2007). Before including water-quality parameters in models, we performed diagnostic checks of data by testing whether there were either influential outliers or collinearity in the data. We chose a pairwise (Spearman) correlation coefficient of (r) > 0.8 as a cut-off (Berry and Felman 1985). To account for over-dispersion and differences in effort between large and small sloughs, we chose to utilize a negative binomial distribution with an offset term for effort. We tested whether independent variables of salinity, temperature, DO, and water transparency (Secchi depth) were significant predictors of catch.

RESULTS

A total of 397,965 overbite clams were captured in 5,508 sampling events at 17 stations over the 27 years. The annual average catch increased significantly over the 27-year period, according

to the Kendall's trend test ($\tau = 0.741$, $p < 0.001$) (Figure 2A). Over 92% of all overbite clams captured in Suisun Marsh were taken from two sites (SU3 and SU4) in lower Suisun Slough (Figures 1 and 2B). Adding catch from the nearby lower Goodyear Slough site (GY3) and the upper reaches of Suisun Slough (SU1 and SU2) accounted for >99% of the total catch (Figures 1 and 2B). Clams were extremely rare in small tidal sloughs, and were less abundant in upstream reaches of larger sloughs than in downstream reaches (Figure 2C).

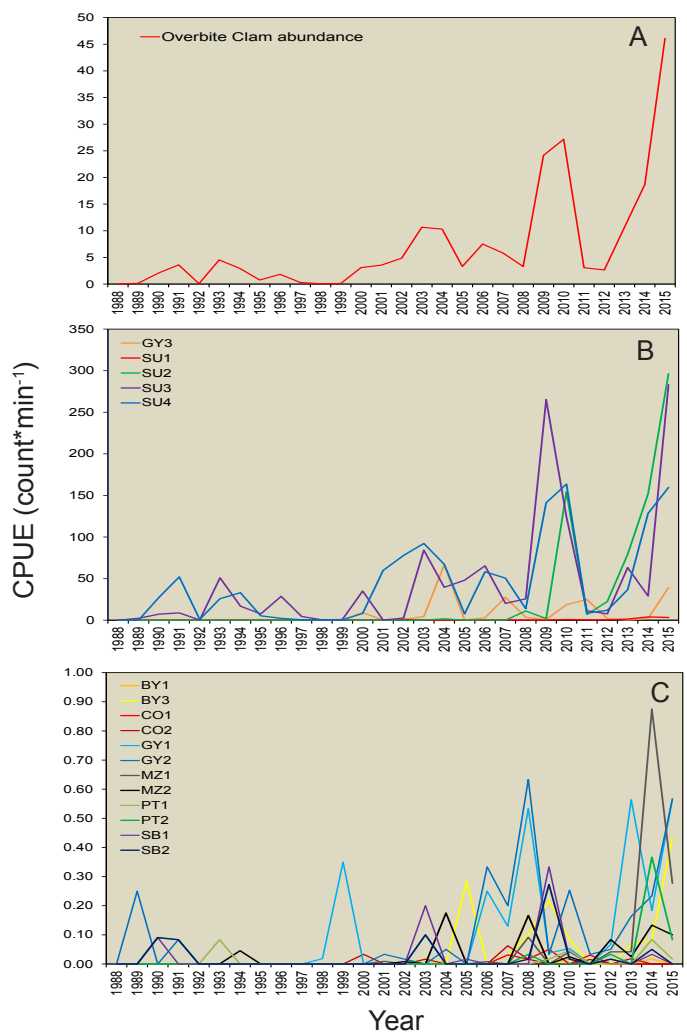


Figure 2 Otter trawl catch of overbite clam in the 17 Suisun Marsh stations sampled over the 27-year period (1988–2015). Catch per unit effort (count per minute) is shown for (A) overall clam abundance over all sites, (B) for the five most abundant sites, and (C) for the remaining 12 non-abundant sites. Note the change in order of magnitude for the Y-axis among graphs.

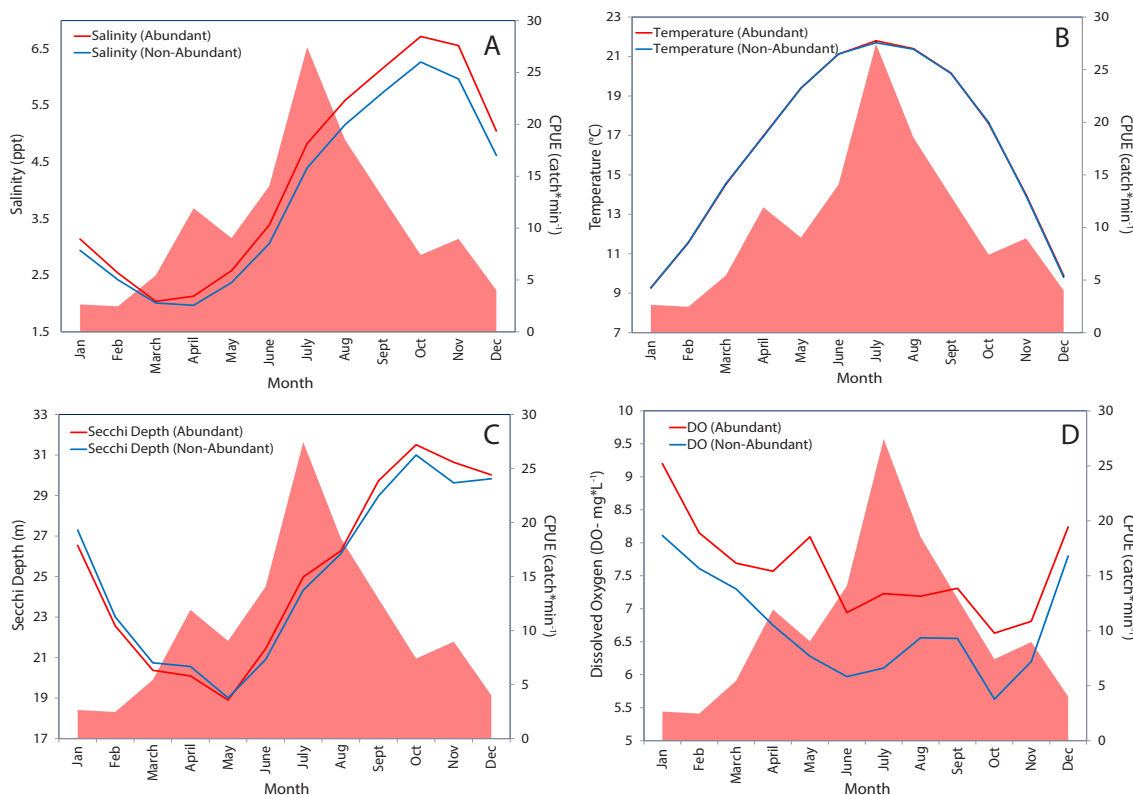


Figure 3 Overall monthly averages over 27 years (16 in DO) for four environmental variables: **(A)** salinity (ppt), **(B)** water temperature (°C), **(C)** Secchi depth (m), and **(D)** dissolved oxygen (DO, mg L⁻¹), grouped into abundant (red) versus non-abundant (blue, *N*) sites. Total abundance (in catch per unit effort [CPUE]) is shown for comparison as the shaded region on the secondary Y-axis. Note that the primary Y-axis has fluctuating values to magnify differences between abundant and non-abundant sites.

Since 2001, the highest proportion of clams caught was generally in spring and summer, with the lowest catch consistently occurring in winter (Figures 3 and 4). Before 2001, catch was lower and highly variable, and no season dominated in any given year, making patterns less apparent (data not shown). Considerable variability since 2000 also existed in the annual catch of clams by site and year because of both the large seasonal fluctuations in catch and the species' limited spatial distribution (Figures A1 and A2, see Appendix A). Abundance in any given month fluctuated from year to year.

The final regression model retained salinity, temperature, and percent-saturation DO as strongly significant ($p < 0.0001$) predictors of clam capture, and accounted for 18% of the total deviance explained (Figure 5). Because the inclusion of Secchi depth (water transparency) was not significant ($p > 0.5$) and only resulted in an additional 1% reduction of the null deviance, it was omitted. The

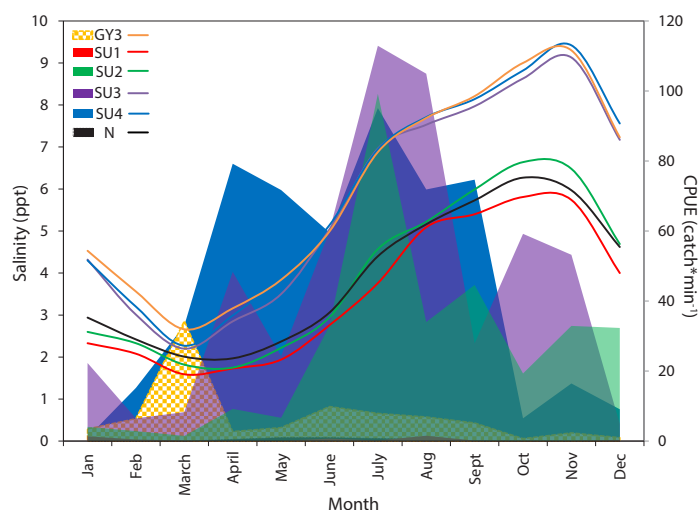


Figure 4 Monthly salinity (lines) compared between the five most abundant clam sites versus the remaining 12 sites (*N*, black line). For further comparison, individual catch per unit effort (CPUE) per site is shaded by matching site color on the secondary Y-axis.

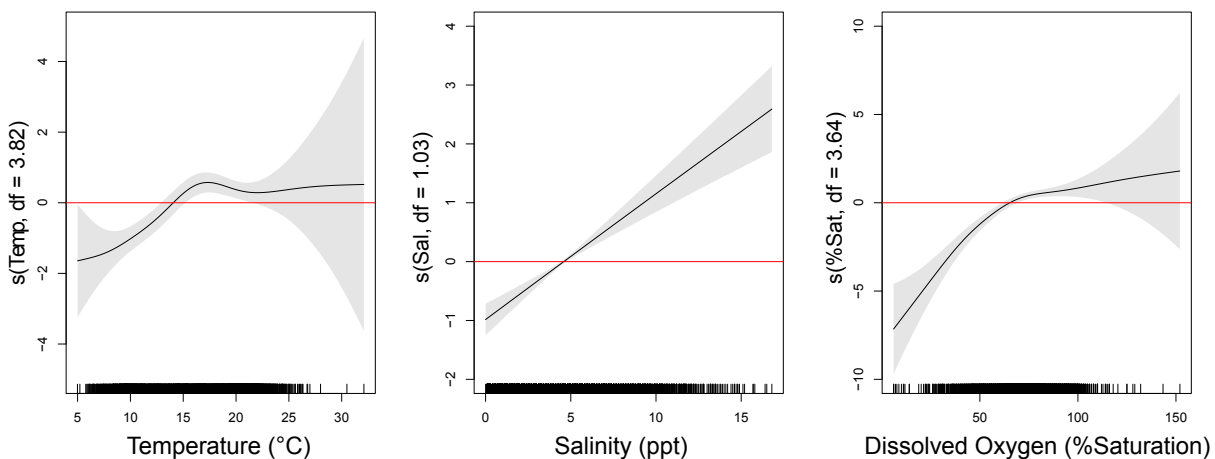


Figure 5 Graphical representation of the smoothed relationship between clam abundance and three environmental variables: temperature, salinity, and dissolved oxygen (% saturation) from generalized additive modeling (GAM). The red line at zero represents when clams are showing neither a positive nor negative response. The degrees of freedom (df) are given for each model on the Y-axis. Black lines along the X-axis denote density of data points.

overall positive increasing relationship among the predicted response for temperature, salinity, and oxygen indicated that clams preferred warm, saltier, well-oxygenated conditions (Figure 5). However, we were unable to assess whether there was an upper bound to this preference, because the abundance of clams did not decline at higher temperatures or salinities. The maximum salinity and temperature measured when clams were captured was 16 ppt and 32.1 °C, respectively.

Plotting average monthly values over the 27-year period of the four environmental variables (16 years for DO) versus abundance (Figure 3; Table A1) revealed little correlation between extreme values of any variable and periods of highest abundance. The exception was water temperature, where the highest average values appeared to coincide with periods of highest catch. Because salinity was the strongest driver in the model, we similarly plotted monthly salinity averages (over 27 years) of the five sites with the bulk of the overbite clams and the 12 other sites with their average abundance values (Figure 4; Tables A2 and A3). Except for the elevated salinities at the three sites with the highest clam abundances (SU3, SU4, GU3), no discernable pattern was evident. Similar results were obtained when we viewed data yearly (Table A4).

DISCUSSION

Overbite clams have progressively increased in abundance in Suisun Marsh since their invasion in 1988, primarily in spring and summer. However, during this period they have maintained a limited spatial distribution, being found mainly in a single large tidal slough: Suisun Slough. The relative lack of spatial shifts in distribution (except in SU2) during this long-term study indicated that most of Suisun Marsh is inhospitable to overbite clams. Modeling results indicated that both clam abundance and distribution were influenced by salinity, water temperature, and DO. Yet, a more fine-scale analysis did not reveal any obvious patterns, which suggests the importance of interactive effects. In addition, as discussed below, to develop a fuller understanding of overbite clams in the marsh, there may have been effects of other factors that need to be studied.

Our study supports salinity as a strong driver of abundance and distribution of overbite clams, as previously documented in other parts of the estuary (Werner et al. 2003). The reported minimum salinity (5 ppt) in Hymanson (1991) corresponds with the optimal range of 5 to 25 ppt for successful spawning and fertilization observed under laboratory conditions (Nicolini and Penry 2000). This minimum salinity matched that of marsh stations that had the highest catch of clams from spring through fall (April–

November). In addition, we documented lower annual average catch when average annual salinity fell below 5 ppt (Figure 3A). However, this finding was in contrast to Miller and Stillman (2013) who found no bio-energetic cost to adult clams that resided in low to moderate salinities (0.2 to 16 ppt). It is likely that our catch patterns of adult clams were partly a result of low salinities that harmed earlier life-history stages, which subsequently reduced recruitment.

In addition to salinity, water temperature and DO were also significant predictors of clam abundance according to our model. The most obvious pattern was the association between the highest average water temperatures and highest abundance (in sites where clams were found), reflected by clams generally being most numerous during summer. Temperature has been an important factor in the distribution and abundance of other related invasive clams (Sousa et al. 2008) and, as for *Corbicula fluminea*, may become more of a factor given ongoing climatic changes (Weitere et al. 2009). However, the correlation between temperature and strong seasonal variations in clam abundance may not be direct and must be viewed cautiously (Viergutz et al. 2012). DO was likewise positively correlated with clam abundance (Figure 5), suggesting that factors contributing to low DO values in the sediments, such as high detrital loads, may restrict clam distribution in the marsh (discussed below).

Although salinity was strongly correlated with the distribution and abundance of overbite clams, the lack of consistent pattern suggests other factors were also important in conjunction with salinity. We propose that the distribution and abundance of overbite clams in Suisun Marsh is the result of a source-sink dynamic. Grizzly Bay is saturated with overbite clams (Greene et al. 2011). Tides likely carry pelagic larvae and dispersing early-stage juveniles with byssal threads (Beukema and de Vlas 1989) into the marsh interior during summer and fall when river outflow is reduced and marine water intrudes into the marsh. However, conditions from winter through late spring in the marsh interior seem to prevent their continued survival to the adult stage. Thus, clam distribution in Suisun Marsh may reflect a balance between colonization from the abundant source populations and the sink of seasonally unsuitable environmental conditions. We hypothesize that three

primary factors contribute to the apparent limitations to recruitment: connectivity, detrital abundance, and predation.

Connectivity

Because Grizzly Bay likely serves as the source for clams in Suisun Marsh, clam abundance should be highest in sites geographically closest to this bay. Also, environmental conditions should be most similar between these sites and the bay. Thus, sites located closest to Grizzly Bay should be repeatedly colonized successfully each year, allowing for increased abundance. This would explain why lower Goodyear Slough (GY3) has had a higher abundance of clams than the upper reaches of Suisun Slough (SU1 and SU2). But the further the distance from Grizzly Bay, the more conditions become sub-optimal, and the fewer individuals that are able to be transported into more distant and smaller sloughs, reducing colonization.

Detrital Abundance

Another possible factor related to the absence of adult clams in small sloughs is the high benthic detrital loads commonly found in these sloughs (unpublished data). High quantities of coarse detritus, which includes leafy debris from tules and other marsh vegetation, may interfere with filter-feeding of clams. The overbite clam is usually partially submerged in bottom sediments and has a short siphon (Carlton et al. 1990), making it vulnerable to smothering by heavy loads of detritus. Thus, juvenile clams would be most vulnerable to this factor, with vulnerability presumably decreasing with increasing clam size. High coarse detritus loads may also either physically dislodge clams as the detritus load shifts with changing tides or contribute to anoxia in bottom sediments. Low DO levels in both sediments and the water column may kill or interfere with reproduction by adult clams and could influence survival of larvae and juveniles. This is supported by the significance of DO in our model.

Predation

Predation may also contribute to observed distribution patterns (Lovvorn et al. 2013). Sacramento Splittail

(*Pogonichthys macrolepidotus*) and White Catfish (*Ameiurus catus*) are both predators of overbite clams (Feyrer et al. 2003; O'Rear 2012) and abundant in Suisun Marsh, particularly within the shallow sloughs of the marsh interior where clams are uncommon or absent (Meng et al. 1994; Matern et al. 2002). White Sturgeon (*Acipenser transmontanus*), another predator of clams (– et al. 2014), inhabits the marsh but primarily within larger sloughs where clams are most abundant. Thus, it is unlikely that White Sturgeon have a large effect on the upstream distribution pattern. Similarly, avian predators—including Greater and Lesser Scaup (*Aythya marila* and *A. affinis*) and Surf Scoter (*Melanitta perspicillata*)—are present in the system but, like sturgeon, are mainly abundant in the downstream reaches of large sloughs near Grizzly Bay (Lovvorn et al. 2013). They are also found in the marsh primarily in winter, when clam populations are at a minimum. Overall, biotic control of clams in the upper and middle reaches of the larger sloughs (i.e., upper Suisun Slough, eastern Montezuma Slough) seems unlikely, but control by fish predation in the smaller sloughs is at least a possibility.

CONCLUSION

To improve performance of restoration projects, the discussion above highlights that more research is needed to determine the mechanisms that make small tidal sloughs unsuitable as habitat for overbite clams. Because salinity is such a strong driver of abundance and distribution of overbite clams, the effect of different freshwater sources on Suisun Marsh—such as Delta outflow (MacWilliams et al. 2015), ephemeral creeks (O'Rear and Moyle 2013), wastewater-treatment discharges (Siegel 2014), and in-marsh water diversions (Laćan and Resh 2016)—should be assessed to elucidate more fine-scale effects of freshwater inflows. Given overbite clam's high filtration rates (Greene et al. 2011), their high abundance in lower Suisun Slough could reduce the supply of phytoplankton and zooplankton transported up the slough from Grizzly Bay to smaller, more interior sloughs. This could be explored via oxygen or sulfur isotopes as indicators of freshwater versus marine origins of production (Leng and Lewis 2016) coupled with overbite clam filtration rates and hydrodynamic models. An intensive survey of overbite clam abundance and distribution in both

Suisun Marsh and Grizzly Bay, combined with shell sizes and reproductive condition, would support or refute our source–sink hypothesis.

In conclusion, the consistent absence of overbite clams in most of Suisun Marsh—especially in smaller sloughs—over the last 2 decades provides strong evidence for the unsuitability of such habitats for them. This allows many areas to remain productive for pelagic fishes such as juvenile Striped Bass (*Morone saxatilis*) and Threadfin Shad (*Dorosoma petenense*), which are routinely captured in the shallow sloughs of the marsh interior (Matern et al. 2002; Schroeter 2008). Other pelagic fishes that may benefit from clam-free areas include Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), Northern Anchovy (*Engraulis mordax*) (Meng and Matern 2001; Matern et al. 2002), and the larvae of many benthic fishes such as Prickly Sculpin (*Cottus asper*). Our findings are also significant for tidal marsh restoration, an important management activity in the estuary. Consistent with Hymanson (1991), our study suggests major invasions by overbite clam into newly restored tidal marshes would be unlikely in regions that experience substantial periods of freshwater inflow.

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